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The life cycle and annual production of *Trichoniscus pusillus pusillus* (Crustacea: Isopoda) in a Cheshire Wood

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With 7 figures

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1. Introduction

The small woodlouse *Trichoniscus pusillus pusillus* Brandt is parthenogenetic and triploid with very rare males, which by reason of their triploidy are sterile (Vandel 1934). Its life history has been described using the method of arithmetical probability paper analysis to determine stadia (Standen 1969). The same material is used here to interpret the life cycle and hence age of a field population. Sutton (1968) has described the size structure and population dynamics of the same species from a limestone grassland in Wytham Wood, Berkshire. The population described is from a deciduous woodland in Cheshire and was studied from 1960–1963 at a time when other investigators were researching various groups of litter and soil dwelling animals at the same site.

2. Description of site

Ernocroft Wood lies twelve miles south east of Manchester (Grid. Ref. SJ/975,910) and rises steeply up the valley of the River Etherow, alt. 300'–450', just above the Etherow-Goyt confluence. Regular sampling was begun in 1959 from two sites in the wood and material from one of these sites was used in the present study. The site is an open stand of sycamore (*Acer pseudoplatanus* L.), and ash (*Fraxinus excelsor* L.) – annual leaf fall was estimated to be approx. 261 Kg/hectare. There is a well developed herb layer consisting of patches of bramble (*Rubus fruticosus* L.) and bracken [*Pteridium aquilinum* (L.) Kuhn] and otherwise a more or less continuous cover of either *Holcus lanatus* L. or *Deschampsia flexuosa* Trin. with *Endymion nonscripta* growing densely amongst both. A fuller description of the site is given by Brookes (1963), Healey (1963, 1964), Fernando (1963), Gabbutt and Vachon (1965) and Blower (1970).

The soil profile is a brown earth and the humus is mull-like moder, *p*H ranging from 4—4.5. The climate of the area is mild and on average most rain falls in August (3.5″) and least in March (2″). The average temperature of the coldest month, January, is 3.4 °C and of the warmest, July 15.8 °C. Just prior to the start of the investigation there was an unusually not dry summer in 1958 and the winter of 1962/3 was exceptionally long and cold. The sample site was a rectangle 30×40 yards (ca. 27.4×36.6 m) divided into 12 squares.

3. Methods

3.1. Sample procedure

On each sampling occasion one litter and one soil sample were taken at random from each square on the grid. The area of soil sample was 1/25 m². The litter sample was collected by volume but the area of the litter removed was noted and was approximately 1/8 m². The temperature of the soil and litter was recorded at each station. The samples were removed to the laboratory and placed on the trays of a Tullgren funnel apparatus which has been described fully by BROOKES (1963). At the temperature regime maintained the process of extraction lasted three weeks. The emerging animals were caught in jars containing dilute copper sulphate solution and the *Trichoniscus* were transferred to 70% alcohol plus glycerine and stored.

3.2. Culture technique

Cultures of *Trichoniscus* were kept in the laboratory for the purpose of studying growth and moulting. The culture chambers were petri dishes containing tap water agar. The relative humidity in the culture at 15 °C was 95%. A hole punched in the agar filled with water gave the animals access to free water considered necessary especially at the time of moulting. The food provided was a disc of leaf litter pressed to the surface of the agar to keep it moist.

3.3. Measurements

Trichoniscus were measured individually using an ocular micrometer attached to a microscope (total magnification ×100). Repeated measurements were within 0.0004 mm. After a series of trial measurements of various parts of the body, the width of the head capsule was chosen as a suitable parameter as it is well sclerotised and unlikely to swell or shrink in different strengths of alcohol.

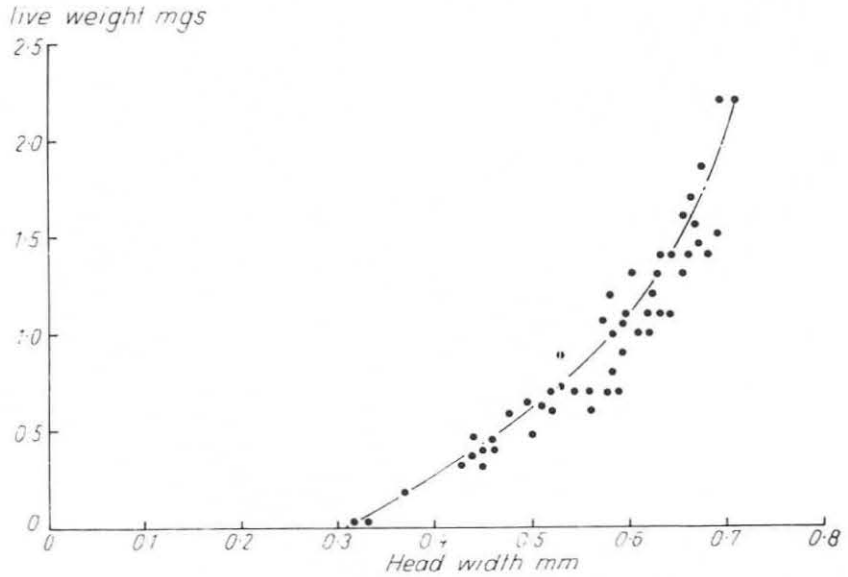

Fig. 1. The relationship between head width (mm) and live weight (mg) in *T. pusillus pusillus*.

T. pusillus pusillus from a woodland in County Durham were measured and weighed using an E. M. B. Electromicrobalance to within 0.01 mg. The relationship between head width and weight shown in Fig. 1 was established from this material, which was then burned in the micro-bomb calorimeter described by PHILLIPSON (1964) to obtain an estimate of the calorific content.

Trichoniscus from Co. Durham were also used to measure the rate of oxygen consumption in a Warburg respirometer. 20—30 individuals were respired in each flask which were 10 m*l* capacity reduced to approximately 7 m*l* by the addition of 3 m*l* glass beads. 0.4 m*l* water was

added to the flask to provide a high humidity and 0.2 ml NaOH in the centre well absorbed the CO_2 evolved. The small glass beads in the flask provided a suitable medium for the animals to rest in. At the end of the experiment all animals were recovered alive and in good condition.

4. Results

4.1. Density and distribution

The total number of *Trichoniscus* extracted from each sample is shown in Table 1. The 12 litter sub-units were each 1/8 m² and multiplied by 8 to give numbers/m². Similarly the 12 soil sub-units which were 1/25 m² in area were multiplied by 25 to give numbers/m². The mean density for each sample is given in Table 2. The mean density ranges from 36 to 300 animals per square metre, the lowest densities occurring just before recruitment in early spring. The highest density in any sample unit was 1,100/m². SUTTON (1968) worked with a much more abundant population at Wytham where he found average densities up to 2,000/m². The number of individuals from any sample unit varied from 0—122 for litter and 0—48 for soil. The variance is high and related to the mean and must therefore be transformed in any procedure using analysis of variance. The high variance of the means obtained most likely results from the aggregation of the animals in the field

Table 1 Mean Number ± S. E. of *T. pusillus pusillus* in each sample

Date	no. of samples	Litter				Soil			
		Total	mean	S. E.	X^2	Total	mean	S. E.	X^2
1959									
20 Oct.	9	44	4.8	0.47	38.8*	20	2.2	0.91	26.9
1960									
18 Jan.	9	39	4.3	3.13	164.6*	62	6.9	2.79	81.6*
1 March	10	13	1.3	0.42	12.46	38	3.8	3.69	322.3*
26 April	12	39	3.2	0.70	31.9*	22		0.52	
16 June	12	61	5.1	1.05		27		0.73	
29 July	12	182	15.2	5.07	222.9*	50	4.2	1.91	114.7*
13 Sept.	12	124	10.3	4.10	215.8*	78	6.5	2.78	157.5*
26 Oct.	12	101	8.4	2.70	96.0*	115	9.6	4.94	335.5*
5 Dec.	12	186	15.5	9.42	755.5*	49	4.1	1.63	355.0*
1961									
6 Dec.	12	90	7.5	2.03	72.9*	146	12.2	4.52	221.4*
1962									
4 April	12	395	32.9	8.65	300.0*	28	2.3	1.06	65.5*
24 July	12	99	8.2	3.21	165.8*	20	1.7	0.41	13.6
26 Aug.	12	77	6.4	1.56	49.7*	17	1.4	0.67	41.6*
22 Sept.	12	30	2.5	0.55	16.3	28	2.3	0.97	54.0*
19 Oct.	12	38	3.1	1.77	134.8*	25	2.1	0.76	36.7*
19 Nov.	12	15	1.2	0.33	11.9	53	4.4	1.45	62.7*
12 Dec.	12	27	2.2	0.80	38.0*	14	1.2	0.67	49.5*
1963									
28 Jan.	12	41	3.4	1.45	81.8*				
4 March	12	101	8.4	3.34	175.7*	24	2.0	0.98	63.8*
21 April	12	40	3.3	0.79	25.0				
14 June	12	107	8.9	3.55	187.2*				
4 July	12	84	7.0	2.14	86.6*	20	1.7	0.69	36.9*
5 Aug.	12	132	11.0	5.09	311.8*	28	2.3	1.16	77.0*

Significance of the degree of aggregation tested by the dispersion index of Fisher $X^2 = \frac{(n-1)\,s^2}{m}$

Table 2 Density of *T. pusillus pusillus* in each litter and soil sample

Date	nos/m²			%
	Litter	Soil	Total	in litter
1959 20 Oct.	38	52	90	42
1960 18 Jan.	32	190	222	14
1 March	11	84	95	12
26 April	26	44	70	37
16 June	41	54	95	42
29 July	108	94	202	54
13 Sept.	82	144	226	36
26 Oct.	76	196	255	23
5 Dec.	115	90	205	56
1961 6 Dec.	53	252	305	17
1962 4 April	242	(56)	298	81
24 July	63	40	103	61
26 Aug.	49	34	83	59
22 Sept.	21	42	63	33
19 Oct.	23	50	73	32
19 Nov.	10	90	100	10
12 Dec.	16	28	44	36
1963 28 Jan.	21	94	115	18
4 March	66	52	118	56
1 April	67	98	165	41
21 April	36	10	46	78
14 June	—	—	—	—
4 July	55	28	83	66
5 Aug.	88	54	142	62

and the dispersion index of Fisher provides a means of testing the significance of the degree of aggregation given by comparing the mean with its variauce (Table 1). Only five litter samples and three soil samples did not show significant aggregation.

Figure 2 shows the percentage of animals in each sample which occurs in litter or soil. In general the majority of animals are in the litter in the summer and in the soil in the winter months. This seems to be a function of temperature as the litter was warmer

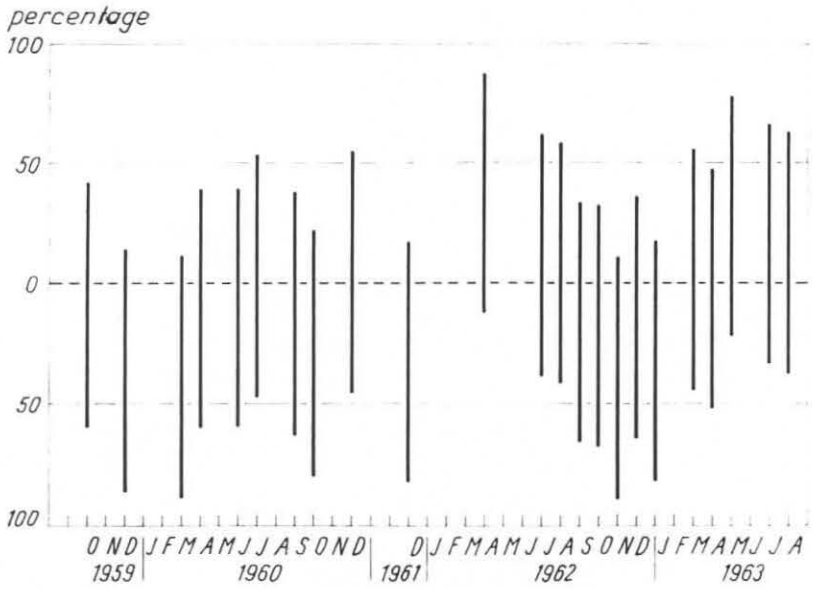

Fig. 2. The percentage of each sample of *T. pusillus pusillus* in litter or soil.

in the summer while the soil was warmer in the spring but most likely the vertical distribution of the animals is also governed by the humidity of the microhabitats and the availability of food. In conditions of extreme drought, in summer, *T. pusillus pusillus* has been found in fissures in the soil at a depth of 30 cms and in these cases the numbers recovered from both soil and litter were low.

4.2. Life Cycle

4.2.1. *Introduction*

The first account of the seasonal changes in a population of woodlice based on systematic field samples was that made by BRERETON (1955) for *Porcellio* spp. and other woodlice in Wytham Wood. A comprehensive study of the population dynamics of *Armadillidium vulgare* (LATREILLE) in grassland in California has been made by PARIS (1963, 1965), PARIS and PITELKA (1962) and PARIS and SIKORA (1965). SUTTON (1968) has given an account of the population dynamics of *T. pusillus pusillus* and *Philoscia muscorum* in limestone grassland of Wytham Wood.

In the present study the samples were taken over a period four years but owing to the lack of extraction apparatus none were taken between January and November 1961 and only three samples were taken in the first half of 1962. Analysis of the samples has shown that the sequence of seasonal change in the age structure of the population of *T. pusillus pusillus* varies from year to year. The flexibility of the epochs in an animal's life in the field may enhance the probability of survival of the population and any factors which appear to influence the variability of the life history stages were of particular interest. Families of *T. pusillus pusillus* were thus maintained in the laboratory for up to two years and provided information on the duration of life history stages under known conditions.

4.2.2. *Breeding*

Ovigerous females first became common at the Ernocroft site in April but animals collected and brought into the laboratory in the preceding three months moulted into the breeding condition within a few days of their transfer. Evidently eggs are present during winter months awaiting the next maternal moult when they are laid into a brood pouch. All field samples from April to December contained some animals with eggs although the proportion ovigerous declines after September. Experiments showed that a period of cold is required to allow a brood to be produced. Animals collected in September and maintained in culture at 10 °C did not produce a brood the following spring while animals kept for one day at − 1 °C moulted into the breeding condition the following March.

The number of eggs or embryos in each brood was established from animals collected by hand to avoid loss of eggs from the brood pouch during the normal extraction process. The estimated correlation coefficient between female head width (x) and number of eggs (y) is high, $r = 0.959$. A line fitted to the points by regression analysis is given by $Y = -28.8 + 58.5\ X$ (Fig. 3).

The eggs are laid into the brood pouch at the time of the moult into the breeding condition. After the brood is released another brood may be produced when the animal next moults or it may revert to the non-breeding condition. There is only one brood per adult stadium and the number of broods produced in a year therefore depends on the number of moults in the year and the percentage of each adult stadium which breeds. Adults taken from each stadium were characterised by analysis of head width and their breeding condition noted. Animals classed as breeding were those with eggs, larvae or young in the brood pouch or those with an empty brood pouch where the young had been already released.

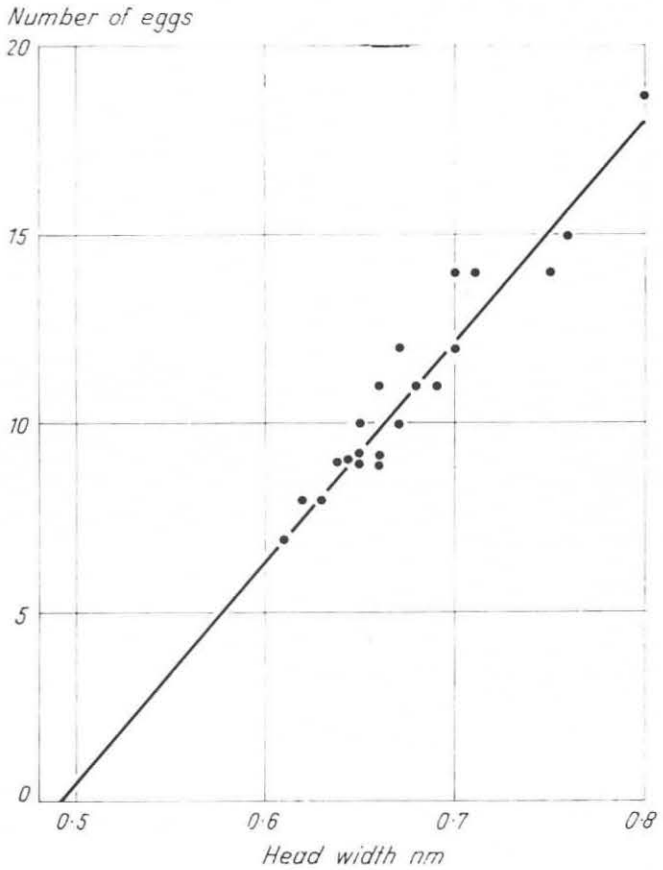

Fig. 3. The correlation between female head width (mm) and the number of eggs in the brood pouch in *T. pusillus pusillus*. Y = − 28.8 + 58.5 X.

4.2.3. *Growth and Moulting*

Growth in woodlice is discontinuous as increase in size takes place at each moult. The mean head width of animals from the field samples was determined by statistical analysis by probability paper (Standen 1969) and the logarithm of mean live weight against stadium number is shown in Figure 4. The ratio of linear dimension as measured by head width per stadium is 1.1 for stadia I—IV but growth per stadium declines after maturity.

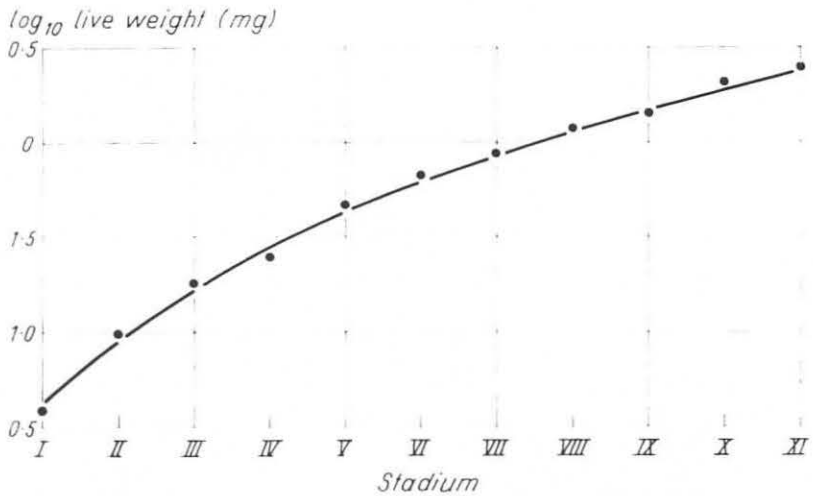

Fig. 4. Growth of *T. pusillus pusillus* expressed as $\log_{10}$ mean live weight of each stadium. Line drawn by eye.

The duration of the juvenile stadia and hence the growth rate varies with temperature. Constant temperature conditions were not available, but families reared in the laboratory in the spring or autumn were compared with those reared in the summer. Cultures were kept in a basement store-room where the maximum and minimum temperature was recorded daily. The duration in days of the juvenile stadia at the average temperature 13.5 °C and 18 °C are shown in Table 3.

Table 3 The duration in days of the juvenile stadia of *T. pusillus pusillus*

	May 1st — Sept. 1st 15—20 °C		Jan. 1st — May 1st and Sep. 1st — Jan. 1st 10—15 °C	
	mean ± S. E.	n	mean ± S. E.	n
Maternal moult — brood release	—		29 ± 0.577	6
Brood release — 1st juvenile moult i. e. stadium I	15 ± 0.563	6	32 ± 3.283	6
Stadium II	25 ± 3.721	6	—	
Stadium III	34 ± 1.258	6	40	2
Stadium IV	35 ± 2.843	5	41 ± 2.182	6
Stadium V	42	2	46 ± 7.364	4
Stadium VI	—		49 ± 3.512	4

4.2.4. *Sequence of moulting and production of broods*

The life history stages of *T. pusillus pusillus* have been described previously (STANDEN 1969). There are six juvenile stadia; the first stadium in which some individuals were ovigerous was stadium VII.

A histogram showing the frequency of stadia in each sample was constructed with the kites smoothed (Fig. 5). The duration of the juvenile stadia was estimated as the distance apart of the peaks of successive stadia. It is important to note that occasionally six weeks elapsed between samples and this is longer than the duration of some of the juvenile stadia.

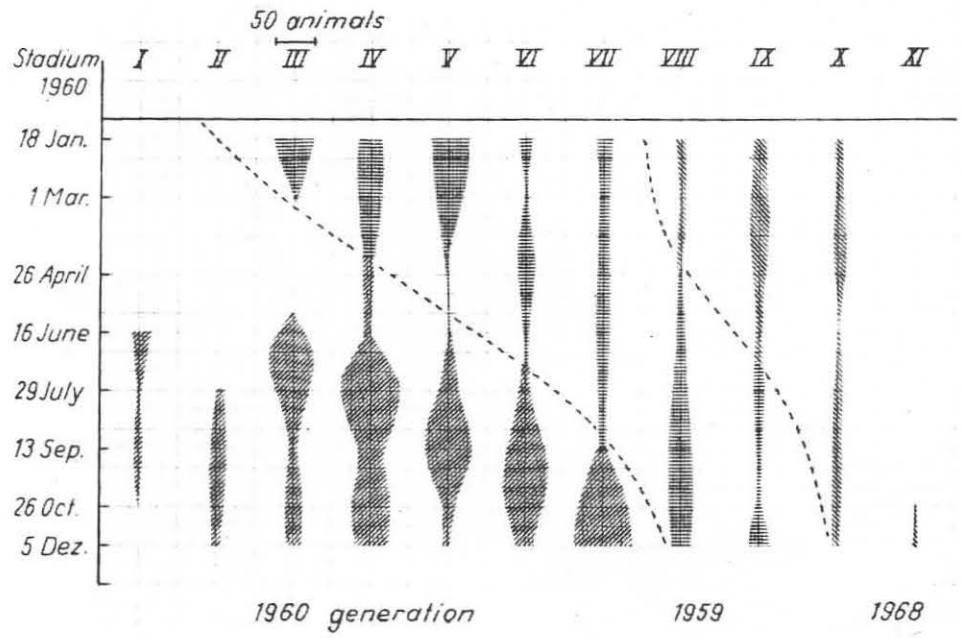

Fig. 5. The number of each stadium in the 1960 samples of *T. pusillus pusillus* shown as histograms with kites smoothed.

Table 4 The main sequence of moulting of the adult stadia of *Trichoniscus pusillus pusillus*

	1960					
	1959 generation				1958 generation	
winter	stadium V				stadium VIII	
26 April	50 %	VII + 0 %	VII − 100 %	50 %	IX + 90 % and X + 100 %	
16 June		VII + 100 %	VII − 0 %			
16 June	52 %	VIII − 80 %	VIII + 20 %	48 %		
29 July		VIII − 25 %	VIII + 75 %			
29 July	52 %	IX + 91 %	IX − 9 %	48 %	54 % X + 70 %	X − 30 % 46 %
23 Sept.		IX + 14 %	IX − 86 %		X + 70 %	X − 30 %
26 Oct.					X + 20 %	X − 80 %

	1963								
	1962 generation							1961 generation	
	1st brood				2nd brood				
winter	stadium VI				stadium IV			VIII−	
4 March	10 %	VII + 10 %	VII − 90 %	90 %	IV			27 % IX + 14 %	IX − 86 % 73 %
1 April		VII + 10 %	VII − 90 %		V			IX + 40 %	IX − 60 %
21 April	50 %	VIII − 90 %	VIII + 10 %	50 %	VI				
16 May		VIII − 10 %	VIII + 90 %	64 %	VII + 66 %	VII − 34 %	36 %	14 % X − 0 %	X + 100 % 86 %
4 July		IX + 100 %			VII + 61 %	VII + 39 %		X − 28 %	X + 72 %

\+ denotes adults in breeding condition

The predominant juvenile stadium overwintering in 1959/60 was stadium V. This moults successively so that the peak abundance of stadium VII is in May 1960. None of the first adult stadium were breeding in the April sample but in June all the first adult stadium present were ovigerous. Also in the June sample were a number of second adult stadia 20% of which were breeding. By July the number of the second adult stadia had increased at the expense of the first adult stadium and 75% were in breeding condition. These second adult stadium animals breeding are assumed to be those which did not breed as first adult stadium earlier in the year. Following the fate of these animals further a decreasing number of first adult stadium occur in September, October and December and 13%, 11% and 0% respectively of these were breeding. There is no evidence as to whether the third adult stadium breeding in July and September were derived from breeding or non-breeding second adult stadium and so it is assumed that both categories contributed equally. The suggested sequence of moulting of the 1959 generation present as adults in 1960 is summarised in Table 4.

Also present in April 1960 were a number of third adult stadium animals, all carrying eggs, which were probably born in 1958 as a second brood. This stadium decreases in abundance in July—September accompanied by an increase in adult stadium 4. Of these 70%, 70% and 20% were ovigerous in July, September and October respectively (Table 4).

The first sample containing ovigerous adults and stadium I was April 26, 1960 and in that season the young are assumed to have been released from the beginning of April. These animals moulted to reach stadium V by the following September by which time more stadium I and II were present and it became clear that there were two peaks in breeding activity in the year. The predominantly juvenile stadia overwintering in 1960 were stadium VII derived from the first brood and stadium IV derived from the second brood.

Systematic sampling ceased in December 1960 and was recommenced in July 1962. At this time stadium III accounted for the majority of the juveniles which then moulted successively to achieve stadium VI by December. Meanwhile another brood had been produced appearing for the first time in the 29 August sample and reaching stadium IV by December.

The first brood of the 1962 generation moult into the first adult stadium at the beginning of March 1963 and 10% of these were breeding. Thus the 1963 breeding season began earlier than in 1960 but the percentage of the first adult stadium which bred was lower. The second adult stadium begins to appear at the end of April. Only 10% were ovigerous but by May all the adults which had moulted into the second adult stadium were breeding; the animals which did not breed as second adult stadia in April are probably those which survived to the third adult stadium, all of which bred.

The second brood of the 1962 generation moult into the first adult stadium in May—July and about 65% breed. The second adult stadium begins to appear in the sample of 5 August.

Some of the reproductive effort of 1963 was derived from animals born in 1961 whose sequeuce of moulting was not followed. These overwintered as the second and third adult stadia and in March and early April 14% and 48% respectively of the third adult stadia were ovigerous. These moulted again and in June and July 100% and 72% respectively were breeding as fourth adult stadium (Table 4).

The first brood of the 1963 generation appeared in 1 April sample and was at a peak at the end of May. These had moulted into stadium III by August 1963 when sampling was discontinued.

4.2.5. *Age structure of the population*

The majority of stadium I are recruited into the population between April and October in two waves with peaks in May and September. They reach maturity sometime between March and August the following year and produce one or two broods the same year. Some survive the following winter to produce another brood in their third year.

The several generations present in the samples can be separated by troughs between stadia illustrated in Fig. 5. The proportion which each generation contributes to each sample is shown in Table 5.

Table 5 The percentage of each generation in each sample of *T. pusillus pusillus* in 1960

Date	1960 generation	1959 generation	1958 generation
1960			
18 Jan.	—	82	18
1 Mar.	—	77	23
26 Apr.	9	60	31
16 June	64	31	5
29 July	75	20	5
13 Sept.	78	18	4
26 Oct.	82	12	6
5 Dec.	75	19	6

4.3. Annual production

4.3.1. *Natality*

T. pusillus pusillus has five adult stadia and the incidence of breeding in these is described earlier and used here to estimate the embryo standing crop. Embryo standing crop on any sample date was calculated as the number of each adult stadium in breeding condition x the average number of embryos per stadium found from the regression equation of number of eggs per brood/female size. Embryo production in a sample interval is then given by

$$\frac{\text{Embryo standing crop}}{\text{development time}} \times \text{sample interval.}$$

The interval between the maternal moult and release of young was 30 days on average at 13 °C and this was taken as the development time. Mortality in the brood pouch was assumed to be negligible as direct examination of the broods revealed either eggs only or larvae only and there is no difference in the regression equation for eggs/female size and larvae/female size. Death of the parents before the young were released could not be estimated and natality was thus taken to be the same as embryo production.

Estimates of the number of embryos produced in the intervals between samples are shown in Table 6.

4.3.2. *Mortality and production in 1960*

The number of any stadium produced is the density in each sample divided by the duration of that stadium. The duration of stadia in the field is difficult to determine. Here as the numbers of one stadium decline and the numbers of the subsequent stadium increase, this is assumed to be due to moulting from one stadium to the next and the time between the peak abundance of successive stadia is taken to be the duration of the stadium. Unfortunately field samples were taken at intervals longer than the duration of some stadia and the peak abundance is estimated from trends. The assumption made here is that there is no mortality factor acting on a particular stadium at a certain period

Table 6 Number of embryos produced by *Trichoniscus pusillus pusillus* in 1960

Date	Stadium	No/m²	No/m² breeding	Embryo standing crop	Embryo production
1960					
26 April	VII	10	—	—	
	VIII	4	4	33.2	
	IX	11	10	100.0	
	X	11	10	120.0	
				253.2	422
16 June	VII	13	13	67.6	
	VIII	10	2	16.6	
	IX	5	—	—	
	X	0	—	—	
	XI	1	—	—	
				84.2	126
29 July	VII	10	4	20.8	
	VIII	20	15	124.5	
	IX	11	10	100.0	
	X	10	7	84.0	
				329.3	495
13 Sept.	VII	10	—	—	
	VIII	23	3	24.9	
	IX	7	1	10.0	
	X	10	7	84.0	
				118.9	132
26 Oct.	VII	70	—	—	
	VIII	27	3	24.9	
	IX	5	—	—	
	X	10	2	24.0	
	XI	6	—	—	
				48.9	59
5 Dec.	VII	80	—	—	
	VIII	15	—	—	
	IX	25	1	10	
	X	12	—	—	
				10	0.3

Average number of eggs of stadium VII = 5.2; VIII = 8.3; IX = 10; X = 12.0; XI = 17.

of its occurrence in the field which would delay the peak abundance of this stadium and thus make the duration of a stadium appear longer than it really is. This assumption is the alternative to the use of the laboratory determined duration of stadia and is preferred in this case where stadia overlap considerably and any particularly heavy mortality is likely to affect more than one stadium.

The calculations of stadium production in 1960 are shown in Table 7, and stadium mortality and annual population turnover in Table 8. Standing crop and annual net production for this year are given in Table 9.

The calorific value of *T. pusillus pusillus* used in the production estimates is 4.019 $\pm$ 0.118/g dry wt. based on 5 burnings of dried animals which were stadia V or VI or adult but not carrying eggs.

The relationship between wet weight and dry weight is shown in Figure 6. There is rather poor correlation between the points (· 8608) and this may be due to the fact that an individual will be in any stage of laying down its next exoskeleton. The ratio of wet

Table 7 Production of stadia of *Trichoniscus pusillus pusillus* in 1960

Stadium	First brood					Second brood				
	Date	No/m²	No/m² X, sample interval	Duration of stadium in field	Stadium production	Date	No/m²	No/m² X, sample interval	Duration of stadium in field	Stadium production
I 1960 Generation	26 Apr.	0	0			29 July	1	45		
	16 June	21	945			13 Sep.	8	352		
	29 July	8	360			26 Oct.	1	37		
			1305	14	93			434	14	31
II	26 Apr.	2	100			29 July	9	405		
	16 June	0	0			13 Sep.	19	836		
	29 July	9	405			26 Oct.	13	481		
			505	28	18			1722	21	82
III	16 June	35	1575			13 Sep.	7	308		
	29 July	40	1800			26 Oct.	20	74		
	13 Sep.	7	308			5 Dec.	12	480		
			3683	128	131			862	21	41
IV	16 June	5	225			13 Sep.	16	708		
	29 July	74	3330			26 Oct.	49	1813		
	13 Sept.	16	704			5 Dec.	31	1240		
			4259	28	152			3757	35	107
V	29 July	20	900							
	13 Sept.	60	2640							
	26 Oct.	10	370							
			3910	35	111					
VI	13 Sept.	50	2200							
	26 ct.	48	1776							
	5 Dec.	20	800							
			4976	50	100					
III 1959						18 Jan.	50	2000	30	
IV Gene-						18 Jan.	36	1440		
ration						1 Mar.	27	1512		
						26 Apr.	a2	600		
								3552	30	118

V						18 Jan.	50	2000		
						1 Mar.	30	1680		
						26 Apr.	1	50		
								3730	60	62
VI						1 Mar.	1	56		
						26 Apr.	15	750		
						16 June	3	135		
								941	60	16
VII	18 Jan.	20	800			26 Apr.	10	500		
	1 Mar.	10	560			16 June	13	585		
			1360	150	9	29 July	10	450		
								1535	90	17
VIII	16 June	10	450			29 July	20	450		
	29 July	10	450			13 Sept.	11	484		
	13 Sept.	11	484			26 Oct.	27	999		
			1384	120	11			1933	100	19
IX	29 July	11	495							
	13 Sept.	7	308							
	26 Oct.	5	185							
			988	90	11					
VIII	18 Jan.	12	480							
	1 Mar.	4	224							
			704	90	8					
IX 1958	18 Jan.	20	800							
Gene-	1 Mar.	15	840							
ration	26 Apr.	11	550							
	16 June	5	250							
			2440	120	20					
X	26 Apr.	11	550							
	16 June	0	0							
	29 July	10	450							
	13 Sep.	10	440							
	26 Octt.	10	370							
	5 Dec.	12	480							
			2290	120	19					

Table 8 *T. pusillus pusillus* population turnover in 1960 (18th January – 5th December)

Stadium	1st brood					2nd brood			
	Live wt. mg.	Stadium production no/m²	no. dying	biomass. mg.	exuvia mg.	Stadium production no/m²	no. dying	biomass. mg.	exuvia mg.
1960									
eggs	0.020	648				686			
I	0.040								
II	0.100								
III	0.180	131	496	42.16	2.11				
IV	0.260	152	– 21	– 0.73	– 0.04	107	579	69.48	
V	0.475	111	41	10.66	0.53				
VI	0.700	99	12	5.70	0.28				
VII	0.850			**57.79**	**2.88**			**69.48**	
1959	1st brood					2nd brood			
III	0.180					150			
IV	0.260					118	32	5.76	
V	0.475					62	56	14.56	
VI	0.700					16	46	21.85	
VII	0.850	12				17	– 1	– 0.70	
VIII	1.250	11	1	0.85		19	– 2	– 1.70	
IX	1.470	10	1	1.25					
				2.10				**39.77**	
1958	1st and 2nd broods								
VIII	1.25	24							
IX	1.47	20	4	5.0					
X	2.00	19	1	1.47					
XI	2.50	2	17	34.00					
				40.47					
Total	209.61 + 10.48 (exuvia) = 220.09 mg.								

Table 9 Standing crop and annual net production in 1960

Stadium	18th January		5th December		
	no/m²	biomass	no/m²	no/m²	biomass
I	0		0	0	
II	11	1.10	4	0.40	
III	50	9.00	12	2.16	
VI	36	9.36	31	8.06	
V	50	23.75	6	2.85	
VI	15	10.50	20	14.00	
VII	20	17.00	80	68.00	
VIII	12	15.00	15	18.75	
IX	20	29.40	25	36.75	
X	8	16.00	12	24.00	
XI					
	222	**131.11**	**205**	**174.97**	

Average biomass B = 113.6 mg = 0.127 Kcals/m²
Annual net production = Annual turnover + difference in standing crop.
= 220.09 + 43.9
= 263.99 mg live wt/m²
= 0.298 Kcals/m²

weight to dry weight is presumably higher just before the moult than just after. An average ratio of wet weight to dry weight of 3.6: 1 is used here and the calorific value of *T. pusillus pusillus* is hence estimated as 1.116 Kcals/g wet weight.

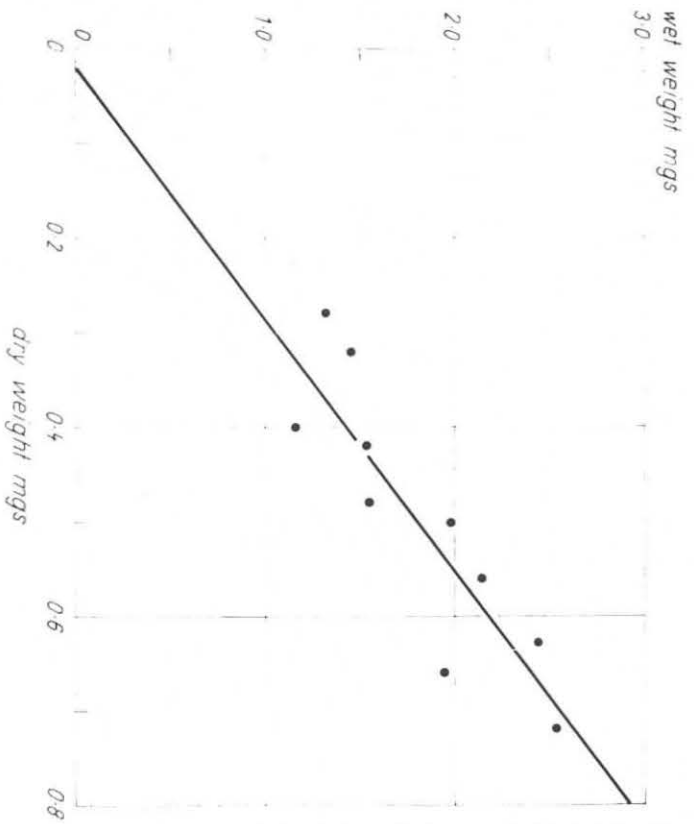

Fig. 6. The relationship between live weight (y) and dry weight (x) in *T. pusillus pusillus*. X= 0.0225 + 0.2642 Y.

4.4. Respiration

The available field temperature data for 1960 are inadequate for an accurate estimate of population respiration to be made, but the respiration in the field has been calculated using the average air temperature at the nearest meteorological station at Ringway Airport, Cheshire. Judging by the known relationship between air temperature and soil temperature (e. g. Moorhouse meterological station) it is likely that the average air

Table 10 Rate of consumption of oxygen by *T. pusillus pusillus* $\mu l O_2$/hr/g live weight

Temp. °C	number of animals	mean weight ± S. E.	oxygen consumption μl O_2/g/hr
5.8	27	1.46 ± 0.10	116.3
	25	1.40 ± 0.16	112.1
	30	1.73 ± 0.12	120.1
	22	1.60 ± 0.12	124.7
			118.3 ± 2.7
10	25	1.70 ± 0.10	265.4
	26	1.66 ± 0.17	243.2
	29	1.63 ± 0.16	268.4
			259.0 ± 7.9
15	27	1.81 ± 0.22	320.1
	29	1.55 ± 0.19	372.9
	29	1.67 ± 0.12	324.0
			339.0 ± 16.8

Table 11 Population Respiration for *T. pusillus pusillus* in 1960

Date	no/m²	biomass mg/m²	°C mean air temp.	μl O_2/hr/g at air temp.	Sample Interval days	μl O_2/hr at field temp. by biomass	μl O_2/m² sample interval
18 Jan.	222	131.1	3	50	42	6.55	6,602
1 Mar.	95	64.3	8	190	56	12.22	16,424
26 Apr.	70	66.7	13	310	51	20.68	25,312
16 June	95	41.9	16	350	43	14.66	15,129
29 July	192	111.4	15	340	46	37.88	41,819
13 Sev.	226	142.5	9	220	43	31.35	32,353
26 Oct.	253	276.4	7	160	40	28.22	27,091
5 Dec.	205	a74.9	4	70	44	12.24	12,925
total							**177,655**

temperatures used are higher than average soil temperatures in summer and lower than the average soil temperatures in winter.

The rate of consumption of oxygen by *T. pusillus pusillus* was determined using a Warburg respirometer. Stadia V, VI or non-breeding adults were collected and stored at the temperature at which they were to be respired. 20—30 weighed animals were then transferred to each flask and their rate of respiration measured at 5.8 °C on 16 March. at 10 °C on 14 June and at 15 °C on 28 June (Table 10). Average rates $\pm$ S. E. were 118.3 $\pm$ 2.69, 259.0 $\pm$ 7.95, and 339.0 $\pm$ 16.8 μl oxygen/hr/g live weight at 5.8 °C, 10 °C and 15 °C respectively.

As the average weights of the animals in each flask were similar there was insufficient data to establish a weight specific relationship.

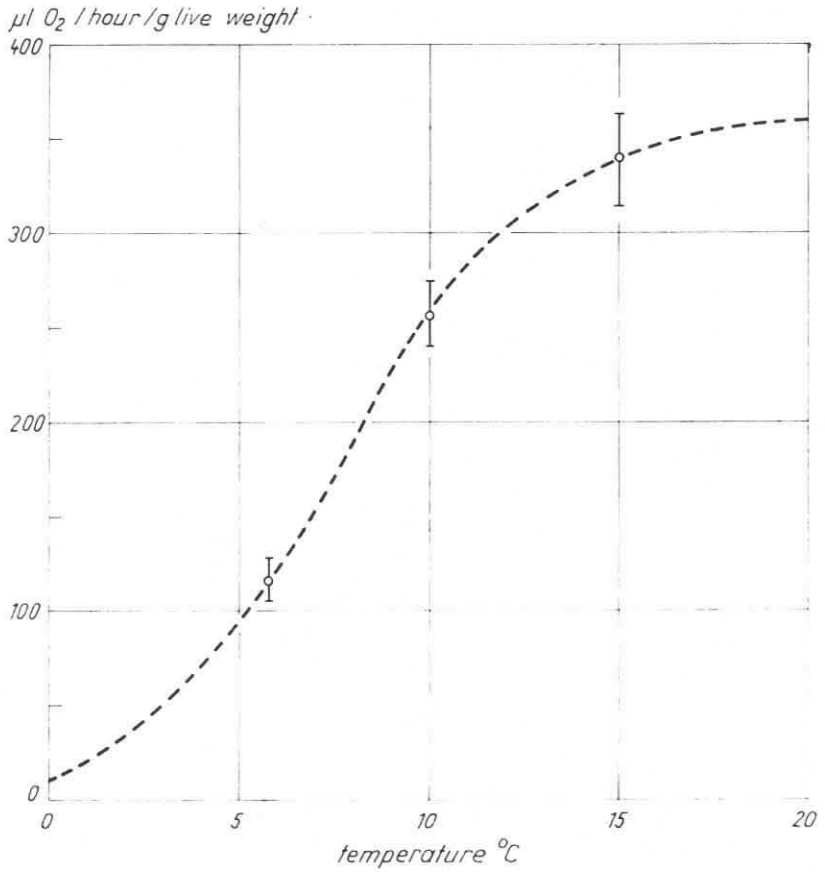

Fig. 7. Mean rate of oxygen consumption $\pm$ 95% confidence limits, by *T. pusillus pusillus* at different temperatures. Line drawn by eye.

An approximate estimate of the annual respiration by the population has been made using the biomass of each sample and the rate of oxygen consumption at the average air temperature for the between sample period, obtained by interpolation in Fig. 7. Population respiration in 1960 was 0.178 litres/m². Using the oxycalorific equivalent of 4,775 Kcals/litre oxygen given by HEILBRUNN (1947, p. 308) — this is 0.850 Kcals/m² (Table 11).

5. Discussion

The characteristics of a population of *T. pusillus pusillus* have been described on the basis of systematic samples of the litter and soil of a woodland taken between October 1959 and August 1963. Subsequently the rate of uptake of oxygen and the relationship between head width and weight were determined using individuals of the same species from Great High Wood, Durham in 1972.

The population studied consisted largely of animals one or two years old. Very few individuals survive to the end of their third year and none to the end of their fourth year. Recruitment into the population is over a very long period. Animals carrying broods were found in the samples as early as 4 March in 1963 and as late as 26 October in 1960. SUTTON's (1968) analysis of the population characteristics of *T. pusillus pusillus* led him to conclude that this extended breeding period was one of the factors which enabled the population to recover numerically after adverse conditions of drought had slowed the growth of juveniles and curtailed breeding. No such period of drought occurred during the present study but the summer previous to its commencement was extremely hot and dry and making use of SUTTON's observations on the effect of drought, this may account for the unimodal structure of the 1959 generation breeding in the summer of 1960 compared to the bimodal structure of the 1962 generation breeding in the summer of 1963 (Table 4). SUTTON (1968) also showed that *T. pusillus pusillus* is not resistant to frost when confined in the upper litter layers in the field. Normally they are able to escape frost and drought by vertical migration. It thus appears that its ecological flexibility in being able to escape adverse conditions enables *T. pusillus pusillus* to survive with reduced growth and recruitment. Its physiological flexibility then allows it to make up for lost recruitment by producing broods into September and October if conditions are more favourable.

The extended recruitment period also makes it difficult to follow the progress of a cohort in order to estimate its survival. The inaccuracy of the calculations which have been made are largely due to this difficulty.

Estimates of annual net production and annual population respiration were confined to 1960 as this was the only year for which data were sufficiently complete. Average standing crop in this year was 0.1136 g/m² (0.127 Kcals/m²) (Table 12). The annual net production in 1960 was 0.2640 g/m² (0.295 Kcals/m²) which is 2.3 times the standing crop.

Table 12 Biomass and energetic parameters of a population of *T. pusillus pusillus* in 1960.

	g/m²	$l\ O_2$/m²	Kcals/m²	
Average standing crop $\bar{B}$	0.114		0.127	
Annual net production P	0.264		0.295	
$P/\bar{B}$				2.3 %
Annual population respiration R		0.178	0.850	
Annual assimilation P + R			1.134	
Annual net population production efficiency $\frac{P \times 100}{A}$				25.0 %

Population respiration was calculated using the total biomass of the sample and the rate of oxygen consumption established for stadium V or VI or non-breeding adult animals. No weight specific rate of respiration was established, and if it is assumed that the relationship between the weight of the animal and the rate of respiration established by PHILLIPSON and WATSON (1965) for *Oniscus asellus* holds for *Trichoniscus* then the estimate of annual population respiration will be low. The ratio of annual net production to the sum of annual net production and annual population respiration $\frac{(P \times 100)}{(P + R)}$ known as annual net production efficiency is 26% which is similar to that given by PHILLIPSON (1967) for *Oniscus asellus*.

LAWSON and MCNEILL (1970) summarise production and respiration data for many species and with reference to these the value of 26% for annual net production efficiency given here lies between the short lived poikilotherms without a resting stage (overwintering active but not productive) and the long lived poikilotherms with two or more active non-productive periods. It has been shown here that *T. pusillus pusillus* suffers heavy mortality in its first six months but may then survive for two winters.

6. Zusammenfassung

Der Lebenszyklus und die jährliche Produktion von Trichoniscus pusillus pusillus (Crustacea: Isopoda) in einem Wald in der Grafschaft Cheshire

Während einer Periode von 3 Jahren wurde in einem Wald von Cheshire eine Population von *Trichoniscus pusillus pusillus* gesammelt. Auf Grund von Ermittlungen über die Fluktuation von Entwicklungsstadien, die zuvor durch Kopfweite-Messungen gekennzeichnet wurden, wurde der Entwicklungszyklus beschrieben.

Es gibt 5 adulte Stadien, die sich vermutlich sukzessiv oder mit einem eingeschobenen Stadium fortpflanzen. Die Schlüpf- und Absterberate der Stadien wurde geschätzt, um den Umsatz der Populationen für ein Jahr und daraus die Netto-Produktion zu ermitteln. Um die Respiration der Populationen kalkulieren zu können, wurden die Respirationsraten der größeren Stadien und der sich nicht fortpflanzenden Adulten in einem Warburg-Respirometer bestimmt. Das Verhältnis der jährlichen Netto-Produktion zur Summe der jährlichen Netto-Produktion + jährliche Respiration der Population ist 26: 100; dieses Verhältnis ist ähnlich dem, das für andere Invertebraten-Populationen ohne Ruhestadium für den gleichen Zeitraum ermittelt wurde.

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